Phylogenetic relationships among 15 sarcophagid fly species (Diptera: Sarcophagidae) based on partial sequences of mitochondrial cytochrome b and cytochrome oxidase subunit Ⅰ genes

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Abstract: In this study, partial DNA sequences of two mitochondrial genes, cytochrome b (Cytb) and cytochrome c oxidase subunit Ⅰ (COⅠ) genes, were used to infer the phylogenetic relationships among 15 sarcophagid fly species, representing the six subgenera of the genus *Sarcophaga* in the catalogue of the Sarcophagidae of the world. The concatenated sequences (972 bp) were employed to carry out the phylogenetic analyses, including MP, ML, and Bayesian analyses. Our results suggested monophyly of three subgenera, *i.e.*, the subgenus *Parasarcophaga*, the subgenus *Boettcherisca*, and the subgenus *Liopygia*. Our analyses also showed that the subgenus *Liosarcophaga* and the subgenus *Pandelleisca* were not monophyletic. This study showed no resolution for the phylogenetic positions of *S.* (*Pandelleisca*) *similis* and *S.* (*Robineauella*) *coei*. Furthermore, the MP analysis and the likelihood function analyses revealed incongruent phylogenetic relationship between the *scopariiformis-iwuensis* clade and the *polystylata-hui* clade. Therefore, other molecular markers and more taxon samplings were needed in the future study.

Key words: Bayesian analysis; phylogeny; cytochrome b (Cytb) gene; cytochrome oxidase subunit Ⅰ (COⅠ) gene

1 INTRODUCTION

The sarcophagid flies, commonly called flesh flies, are a group of large-sized, mostly grayish, calypterate flies, with 2 510 valid species in 108 genera being recorded (Pape, 1996). Some members of the group have been extensively used for the study of the antibacterial peptide, lectin and the estimation of the postmortem interval (PMI). However, fossils and molecular data available with respect to the sarcophagid flies are very limited. Up to now, neither cladistic analyses nor molecular evidences can be used to support the generic classification, saying nothing of the interspecific relationships within a genus. Here, we use the molecular markers to investigate the phylogenetic relationships among 15 sarcophagid flies (Table 1) and attempt to address their taxonomic problems that remain strongly controversial in different taxonomic classifications.

Based on the investigation of the sarcophagid flies from the Oriental region, Lopes *et al*. (1977) had ever reported 33 species within the genus *Parasarcophaga* (s. st.) and ranged them into seven subgenera. According to Lopes' classification, 11 taxa in this study (no record for *S.* (*Pan.*) *polystylata* and *S.* (*R.*) *coei* at that time) were arranged into five subgenera of the genus *Parasarcophaga* (s.st.) (Table 1).

In the Key to the Common Flies of China edited by Fan (1992), the 13 taxa were assigned to the genus *Parasarcophaga* (s.st.) and the two taxa were placed in the genus *Boettcherisca* (s.st.). According to the Key to the Genus *Parasarcophaga* in the Fan (1992), the relationships among the 13 taxa in the genus *Parasarcophaga* can be simply depicted using the hand-made cladogram shown in Fig. 1a.

In the Checklist of *Sarcophagidae* (Diptera) recorded from China (Fan and Pape, 1996), the 15 taxa of this study represented six genera of the tribe *Sarcophagini* (s. st.). In the Catalogue of the Sarcophagidae of the World (Pape, 1996), they were arranged to six subgenera of the genus *Sarcophaga* (s. lat.). By comparison, there was only one difference between them. That is, different taxonomic concepts

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Table 1 List of taxa and their GenBank accession numbers in this paper

Family	Genus/Subgenus/Species (Lopes *et al.*, 1977)			Subgenus/Species (Pape, 1996)		GenBank accession no. (*COI*)	GenBank accession no. (*Cytb*)	References
Sarcophagidae	*Parasarcophaga*	*Parasarcophaga*	*albiceps*	*Parasarcophaga*	*albiceps*	AY879247	AY879232	This study
			orchidea (*misera*)		*misera*	AY879257	AY879240	This study
			knabi (*sericea*)		*sericea*	AY879260	AY879241	This study
		Pandelleisca	*hui*	*Pandelleisca*	*hui*	AY879258	AY879239	This study
			similis		*similis*	AY879256	AY879244	This study
		Liosarcophaga	*brevicornis*		*iwuensis*	AY879259	AY879245	This study
			misera (*dux*)		*polystylata*	AY879252	AY879235	This study
			iwuensis	*Liosarcophaga*	*brevicornis*	AY879251	AY879234	This study
			scopariiformis		*dux*	AY879255	AY879242	This study
		Liopygia	*ruficornis*		*scopariiformis*	AY879250	AY879233	This study
		Jantia	*crassipalpis*	*Liopygia*	*crassipalpis*	AY879254	AY879238	This study
					ruficornis	AY879253	AY879237	This study
				Robineauella	*coei*	AY879261	AY879236	This study
	Boettcherisca		*formosensis*	*Boettcherisca*	*formosensis*	AY879249	AY879243	This study
			peregrina		*peregrina*	AY879248	AY879246	This study
Calliphoridae			genus *Chrysomya*		*putoria*	AF352790	AF352790	Junqueira *et al.* (2004)

The *orchidea* and *knabi* are the senior synonyms of *misera* and *sericea* in the brackets respectively. The *misera* has ever been used as the junior synonym of the *dux* in the bracket.

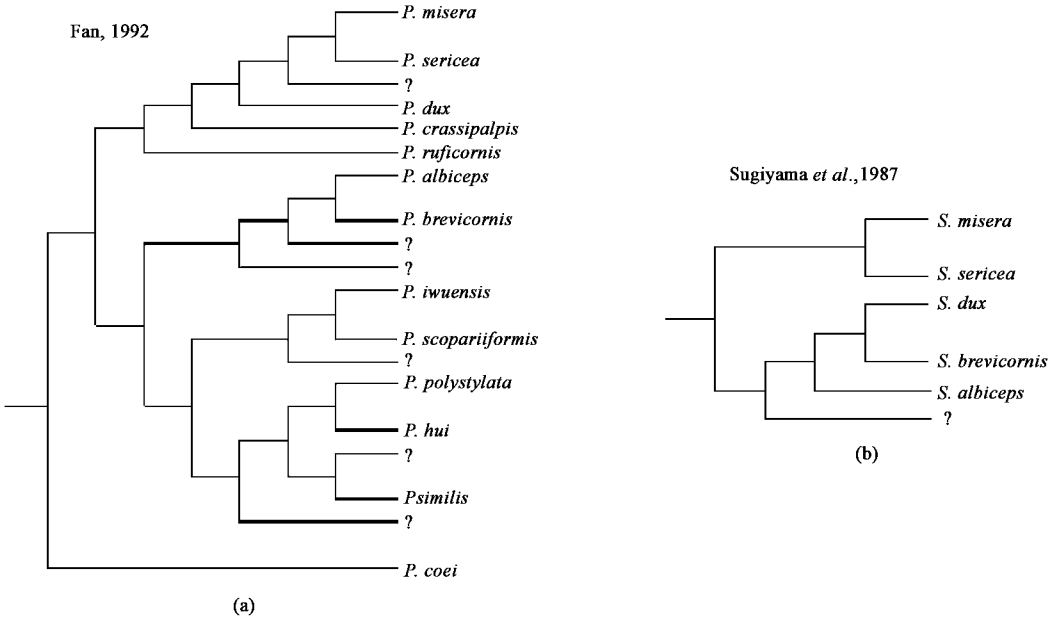

Fig. 1 Hand-made cladograms based on the keys in Fan (1992) (a) and Sugiyama *et al*. (1987) (b).
The question marks in the trees indicate the absence of taxa sampling.

were used to define the high ranks above the species level.

As related above, morphological taxonomies give the controversial positions for the 15 sarcophagid fly species. Therefore, it is necessary to test different morphological hypotheses using molecular data. Here we are not concerned about the conceptual difference between systematists because that is uncontroversial in the phylogenetic sense. We focus on the interspecific relationships and which genus or subgenus each species should belong to. Another aim of this study is to examine the monophyletic origin of each genus. Two mitochondrial (mt) genes, cytochrome C oxidase subunit Ⅰ (COⅠ) gene and cytochrome b (Cytb) gene, have been chosen as phylogenetic markers because recent studies have shown that partial sequences of COⅠ and Cytb genes contain useful information in resolving phylogenetic relationships among species and subgenera of the Dipteran insects (Guryev *et al*., 2001; Papoucheva *et al*., 2003).

2 MATERIALS AND METHODS

2.1 Taxa examined

The 15 sarcophagid flies were identified using the structure of male terminalia with other outer morphological characters. The male terminalia of these taxa had been deposited in the Insect Collection of Natural Museum of Sun Yat-Sen University as voucher specimens. The species *C. putoria* was chosen as outgroup and its sequences were downloaded from GenBank. Table 1 listed the taxa used in this study along with GenBank accession numbers for each sequence.

2.2 DNA extraction, amplification and sequencing

Genomic DNA was isolated from thoracic muscle following the method below: Single specimen (dry, freezing or ETOH) was firstly dipped in 400 – 1 000 μL TE buffer (pH 7.0) and incubated at 37℃ water bath for over 1 h. Thoracic muscle was dissected out and ground with 200 μL TEN9 (50 mmol/L Tris-Cl, 100 mmol/L EDTA, 200 mmol/L NaCl, pH 9.0) in a 1 mL-glass homogenization vessel. After adding 11 μL SDS (20%) in the homogenating liquid and pretreating the mixture about 10 minutes on ice, then adding 2.5 μL proteinase K (20 mg/mL), the total mixture was incubated at 55℃ water bath overnight. The following DNA extraction was performed according to the standard phenol/chloroform methods. The total DNA was redissolved in 50 – 100 μL sterilized double distilled H_2O.

The COⅠ and Cytb gene fragments were amplified using the following primer pairs designed with the software Primer Premier 5.0 based on complete genome of *Drosophila yakuba* mitochondrion (GenBank accession number NC_001322): (1) COX1_sf856 (5′-ACT TGT AAA TAT ATG ATG ATC TCA-3′) (2 329 – 2 351) and COX1_af281 (5′-CGA ATA AAT AAT ATA AGA TTT TGA-3′) (1 753 – 1 776) for the COⅠ gene fragments and (2) CytB_s401 (5′-TAC CTT GAG GAC AAA TAT CAT TTT-3′) (10 915 – 10 938) and CytB_a878 (5′-ATA ACT CCT CCT AAT TTA TTA

GGA AT-3′) (11 367 – 11 392) for the Cytb gene fragments. The bold digits in the brackets were used to mark the initial and terminal positions of the primers in the complete genome of *D. yakuba* mitochondrion. PCR amplification was carried out in 60 μL reaction volume using the standard technique with Taq polymerase at the annealing temperatures of 42℃ for CO Ⅰ gene and 45℃ for Cytb gene. PCR products were isolated from agarose gel using the E.Z.N.A.® Gel Extraction Kit (Omega) and then sequenced directly for both forward and reverse DNA strands. All automated sequencing was conducted using AB APPLIED Biosystems/ HITACHI ABI3730 DNA Analyzer.

2.3 Sequence availability and alignment

Newly generated sequences in this study had been deposited in GenBank. Firstly, the forward and reverse primer sequences were trimmed out from raw sequences using the program EditSeq of the software package DNAStar. And then Blastn and Blastx were employed to determine the direction of sequences and to locate coding region. We obtained partial nucleotide sequence of the two genes (552 bp from CO Ⅰ gene and 420 bp from Cytb gene) without initiation and stop codons. Both partitions were aligned respectively using CLUSTALX1.81 with the default settings. The aligned data sets were reproducible using the method described above, but were also available as Nexus or MEGA file from the authors upon request.

2.4 Data analysis

Base frequencies and Chi-square test of homogeneity of base frequencies for each gene fragment were calculated with PAUP* 4.0b10 (Swofford, 2002). Saturation analyses were performed to assess the levels of multiple substitutions at the third codon position for each locus as described by Griffiths (1997). Partition homogeneity test (PHT; Farris *et al*., 1994, 1995) contained in the PAUP* 4.0b10 was used to test the incongruence between both partitions (heuristic searches, 1000 replicates).

Maximum parsimony (MP) and maximum likelihood (ML) analyses were conducted using PAUP* 4.0b10. MP analyses were carried out using the heuristic search procedures, with the tree-bisection-reconnection (TBR) employed as branch-swapping algorithm and starting trees obtained via random stepwise addition. All characters were treated as unordered. Bootstrap values were obtained with 1 000 replicates.

Maximum likelihood (ML) analyses were performed as follows: (1) the appropriateness of different models was estimated using the program Mrmodeltest 2.0. (Nylander, 2004); (2) the parameter values of the model estimated above including nucleotide frequencies, number of substitution types, rate matrix, distribution of rates at variable sites, shape parameter and proportion of invariable sites were directly applied in the likelihood search (search type = heuristic, addition sequence = as is). Support for each clade in the ML tree was determined using bootstrap proportions. One hundred replicates were performed for each locus.

Bayesian phylogenetic analyses were implemented using MrBayes v.3.1 program (http://mrbayes.net) on computers running Windows 2000. The program Mrmodeltest 2.0 was also used to select the setting parameters for each run. Bayesian posterior probability (PP) was determined from the phase where the likelihood values had reached stable phase beyond the burnin (=250, in this study) phase.

3 RESULTS

3.1 Data characteristics

Mean base frequencies for the ingroups and outgroups demonstrated that nucleotide composition of each locus biased towards As and Ts. The average A + T content was 68% for CO Ⅰ (A = 29.5%, C = 16.4%, G = 15.6%, T = 38.5%) and 71.6% for Cytb (A = 31.2%, C = 17%, G = 11.4%, T = 40.4%), which corresponded to the characteristics of the base composition of the mitochondrial genome of other Diptera insects (ranged from 72.6% to 82.2%) (Junqueira *et al*., 2004). No significant differences were detected between the base frequencies across the taxa (the P value for each locus equals to 1.0).

Up to 103 of 128 variable sites of the Cytb gene fragment and 129 of 151 variable sites of the CO Ⅰ gene fragment distributing at the third codon position suggested that multiple substitutions possibly occurred at a majority of the third codon positions of the two loci. To further examine the nature of the third codon position variation, we used saturation analyses to test noise data with relation to substitution. Paired Student t-tests (all P values less than 0.01) showed that the transitions and transversions at the third codon position were unsaturated. Therefore, all sites of the two gene fragments would be used to carry out phylogenetic analyses.

3.2 Phylogeny

We concatenated the Cytb and CO Ⅰ data sets to reconstruct phylogenetic trees because: (1) the PHT indicated that the molecular partitions forming the concatenated matrix are not significantly incongruent (p = 0.349); (2) the concatenated data set provides additional characters for the recovery of a meaningful phylogeny (Guriev *et al*., 2001); (3) combined

approaches are helpful in improving phylogenetic accuracy and resolution based on more characters (Hillis, 1996).

The MP analysis produced one parsimonious tree (Fig. 2a) of length 595 steps with 195 parsimony-informative characters. The consistency index (CI) of the MP tree was 0.556, with retention index (RI) of 0.539. The MP analysis strongly supported monophyly of the three clades including the *Parasarcophaga* clade, the *Boettcherisca* clade, and the *Liopygia* clade (bootstrap values ≥ 94%) and suggested such interior relationships as (*S.* (*Par.*) *albiceps*, (*S.* (*Par.*) *misera*, *S.* (*Par.*) *sericea*) for the *Parasarcophaga* clade. Several sister relationships between some of the species (*e. g. S.* (*Lios.*) *scopariiformis* and *S.* (*Pan.*) *iwuensis*, *S.* (*Pan.*) *polystylata* and *S.* (*Pan.*) *hui*, *S.* (*Lios.*) *brevicornis* and *S.* (*Lios.*) *dux*) were also revealed in the MP analysis. Simultaneously, the MP phylogenetic tree recovered the paraphyletic relationship between the *scopariiformis-iwuensis* clade and the *polystylata-hui* clade. The MP analysis showed no resolution for the phylogenetic positions of *S.* (*Pan.*) *similis* and *S.* (*R.*) *coei*.

The GTR + I + G model was selected as the best-fit model by hLRT in MrModeltest 2.0 for the ML analysis. The estimated value of proportion of invariable sites (P_{invar}) was 0.6001, with the gamma shape parameter of 1.9423. The ML phylogenetic tree was shown in Fig. 2b, with a best tree score of 2 986.70. The ML tree topology was similar to the MP tree topology except that the *scopariiformis-iwuensis* clade and the *polystylata-hui* clade formed a monophyletic group.

The hLRT in MrModeltest 2.0 selected the

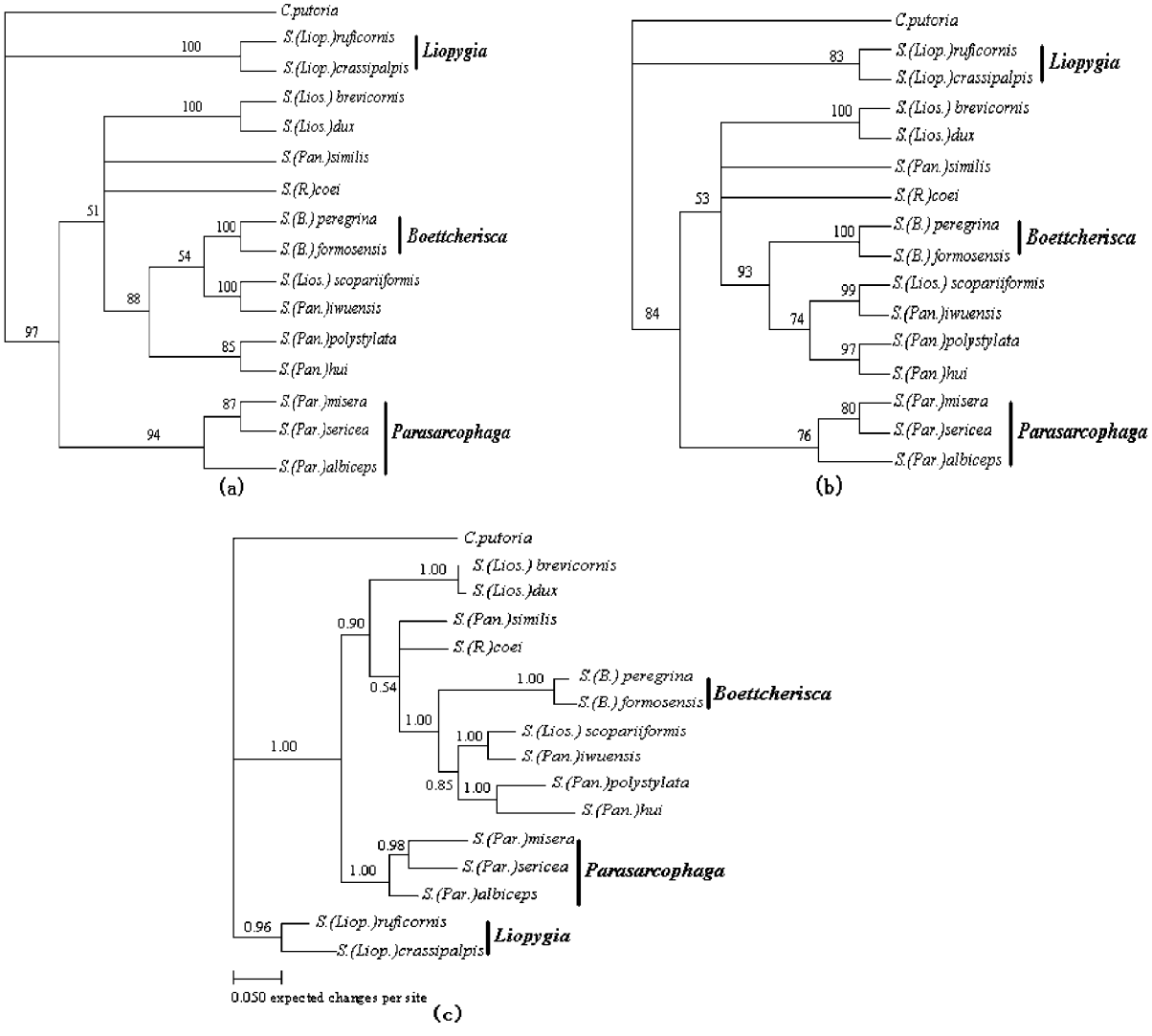

Fig. 2 Phylogenetic reconstruction based on the concatenated data sets.
(a) MP method, (b) ML method, and (c) Bayesian method.
Numbers above the branches indicate bootstrap percentages (BP) and posterior probabilities (PP).

following parameters for the Bayesian analysis: statefreqpr = dirichlet (1, 1, 1, 1), nst = 6, rates = invgamma. These parametric settings also corresponded to the GTR + I + G model. The Bayesian result was given in Fig. 2c. All branch lengths were drawn proportional to the number of substitutions per site. The Bayesian analysis basically yielded the same tree topology as the ML analysis. The Bayesian tree seemed to give the rough resolution for the phylogenetic positions of *S*. (*Pan*.) *similis* and *S*. (*R*.) *coei* because the ML bootstrap percentages are more conservative than the Bayesian posterior probabilities in estimating the reliability for the clades (reviewed in Gontcharov *et al*., 2004).

4 DISCUSSION

Our analyses present a primary hypothesis for the phylogenetic relationships among 15 sarcophagid flies based on the concatenated data sets of both molecular partitions.

Sugiyama *et al*. (1987) had ever identified sister relationship between *S*. (*B*.) *formosensis* and *S*. (*B*.) *peregrina* using several characters such as hind tibia without long hairs. Our analyses argue with the taxonomic classification. Previous morphological studies (Rohdendorf, 1937, 1965; Verves, 1986; Fan, 1992) suggested that the "central" genus *Parasarcophaga* (s. st.) was not a natural species group due to the absence of the distinct generic characters. The nested phylogenetic positions of the *Boettcherisca* clade in the gene trees recover polyphyly of the "central" genus *Parasarcophaga* (s.st.).

Monophyly of the *Liopygia* clade in all analyses indicates that *S*. (*Liop*.) *ruficornis* is very closely related to *S*. (*Liop*.) *crassipalpis*. Our results are in agreement with previous molecular phylogenetic analyses (Wells *et al*., 2001). In contrast to different morphological hypotheses, present analyses agree with the taxonomic classifications both in Pape (1996) and in Fan and Pape (1996), but argue against the relationship between the two species suggested by Fan (1992) and Lopes *et al*. (1977).

All gene trees show that the *brevicornis-dux* clade is polyphyletic in relation to the *scopariiformis-iwuensis* clade, suggesting that the subgenus *Liosarcophaga* in the Pape (1996) is polyphyletic; so is the subgenus *Liosarcophaga* defined in the Lopes *et al*. (1977). Fan (1992) considered that *S*. (*Lios*.) *brevicornis* was very distinct from *S*. (*Lios*.) *dux* (Fig. 1a). Contrary to Fan (1992), Sugiyama *et al*. (1987) suggested sister relationship between *S*. (*Lios*.) *brevicornis* and *S*. (*Lios*.) *dux* based on the characters of the sixth abdominal tergite and the juxtal process. Our analyses also show that *S*. (*Lios*.) *brevicornis* and *S*. (*Lios*.) *dux* are able to stably form a sister species group. Monophyly of the *scopariiformis-iwuensis* clade suggests that *S*. (*Lios*.) *scopariiformis* is closely related to *S*. (*Pan*.) *iwuensis*, which agrees with previous morphological studies (Sugiyama *et al*., 1987; Fan, 1992).

Molecular analyses show that four representatives of the subgenus *Pandelleisca* (Table 1) in the Pape (1996) cluster into three clades, *i*. *e*. the *similis* clade, the *scopariiformis-iwuensis* clade, and the *polystylata-hui* clade (Fig. 2). Our analyses show no resolution for the status of *S*. (*Pan*.) *similis*. Furthermore, the species *S*. (*Pan*.) *iwuensis* displays paraphyletic relationship with respect to the *polystylata-hui* clade. These suggest that the subgenus *Pandelleisca* in the Pape (1996) is not monophyletic but polyphyletic. Moreover, no evidence in our analyses supports sister relationship between *S*. (*Pan*.) *similis* and *S*. (*Pan*.) *hui*, which rejects the morphological definition of the subgenus *Pandelleisca* in the Lopes *et al*. (1977). The MP tree (Fig. 2a) recovers the paraphyletic relationship between the *scopariiformis-iwuensis* clade and the *polystylata-hui* clade whereas the ML and Bayesian trees (Figs. 2b and 2c) suggest the monophyletic relationship between them, whichever relationship is not in agreement with the taxonomic relationship proposed by Fan (1992).

The *Parasarcophaga* clade consists of the three species, *i*. *e*. *S*. (*Par*.) *albiceps*, *S*. (*Par*.) *misera*, and *S*. (*Par*.) *sericea*. All gene trees unambiguously recover monophyly of the *Parasarcophaga* clade, supporting monophyly of the subgenus *Parasarcophaga* in the Pape (1996) and in the Lopes *et al*. (1977). Although the monophyly of the *Parasarcophaga* clade conflicts with the taxonomic classifications proposed by Fan (1992) and Sugiyama *et al*. (1987), the sister relationship between *S*. (*Par*.) *misera* and *S*. (*Par*.) *sericea* inferred from our analyses agrees with their taxonomic viewpoints (Figs. 1a and 1b).

The likelihood function analyses (*i*. *e*. ML and Bayesian analyses) and the MP analysis produce the incongruent phylogenetic resolutions for the relationship between the *scopariiformis-iwuensis* clade and the *polystylata-hui* clade. KHTEST (Kishino and Hasegawa, 1989; khtest = rell, tailkh = 1) and SHTEST (Shimodaira and Hasegawa, 1999; shtest = rell) indicate that there are no significant differences between the MP and the ML tree topologies (K-H, P = 0.219; S-H, P = 0.219). We present a rough

explanation for this conflicting phenomenon based on previous theories. Separate analyses of the Cytb and CO Ⅰ data sets (Fig. 3) reveal the same conflict as mentioned above. Reed and Sperling (1999) considered that this conflict between both molecular partitions might be ascribed to different evolutionary history of both partitions. Theorists have also argued that the combined data tree topology are influenced by the strength of the "signals" of different partitions which might be swamped or compromised each other in the combined analysis (Hipp *et al.*, 2004; Reed and Sperling, 1999). The bootstrap percentages (BP) can be used as the rough indicators of the signals within data partitions (Reed and Sperling 1999; Sanderson *et al.*, 2000). In the single-gene MP analyses, the CytB data set provides weaker phylogenetic signals (BP = 49%) for the monophyletic relationship between the *scopariiformis-iwuensis* clade and the *polystylata-hui* clade while the CO Ⅰ data set suggests the paraphyletic relationship between them with a strong phylogenetic signals (BP = 74% for the node shared by the *scopariiformis-iwuensis* clade and the *Boettcherisca* clade). It is possible that the strong CO Ⅰ signals for paraphyly swamps the weaker Cytb signals for monophyly in the combined MP analysis. However, the phylogenetic signals of the Cytb and CO Ⅰ loci in the ML analysis are adjusted adversely due to the application of the substitution models and the Gamma distributions. Unfortunately, a heterogeneous substitution model is not used in the combined ML analysis in this study. The detailed studies, *e. g.* constructing a heterogeneous model (Pupko *et al.*, 2002) and detecting conflicting phylogenetic signals using likelihood ratio test (Huelsenbeck and Bull, 1996), fall out of the scope of this work.

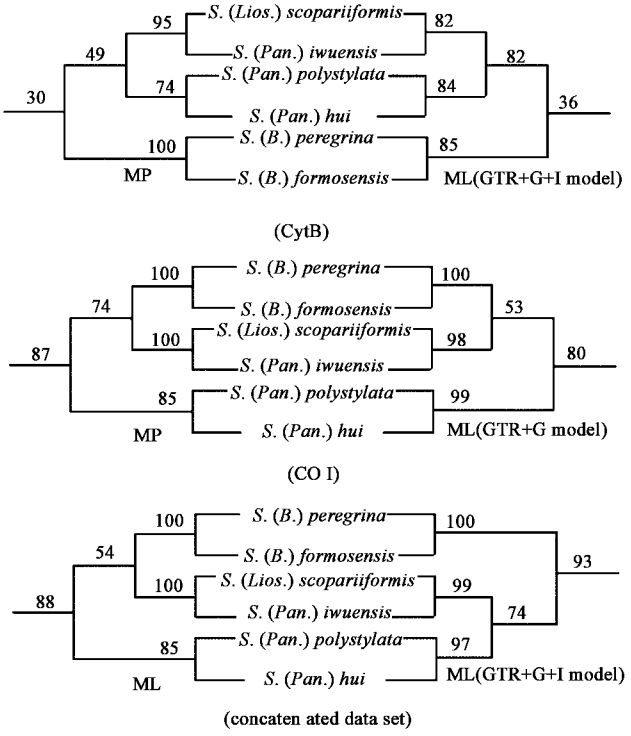

Fig. 3 Comparison among the subtrees yielded from the Cytb, CO Ⅰ, and concatenated data sets, respectively. Numbers above the branches indicate bootstrap percentages.

In summary, our study provides some useful insights into the taxonomy of these species. Several sister relationships and monophyly of the *Parasarcophaga* clade are uncontroversial in our analyses. Nonetheless, present analyses are still powerless in clarifying the relationship between the *scopariiformis-iwuensis* clade and the *polystylata-hui* clade and the phylogenetic positions of *S.* (*Pan.*) *similis* and *S.* (*R.*) *coei*. Therefore, more sequence information and more taxa sampling are needed to resolve the incongruent and unclear phylogenies.

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基于 Cytb 和 COⅠ基因部分序列的 15 种麻蝇之间的系统发育关系（双翅目：麻蝇科）

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摘要：本研究通过测序 Cytb 基因和 COⅠ基因的部分序列来推定 15 种麻蝇之间的系统发育关系。在世界麻蝇名录中，本研究的 15 种麻蝇能够代表麻蝇属 *Sarcophaga* 的 6 个亚属。连接序列（972 bp）被用于系统发育分析，分析方法包括了了最大简约法、最大似然法以及贝叶斯法。我们的结果提示了亚麻蝇亚属 *Parasarcophaga*、别麻蝇亚属 *Boettcherisca* 以及红麻蝇亚属 *Liopygia* 的单系性，同时也表明蛇麻蝇亚属 *Liosarcophaga* 和德麻蝇亚属 *Pandelleisca* 并不是单源的。不过，目前的研究并不能分辨野德麻蝇 *S.*（*Pandelleisca*）*similis* 和峨眉叉麻蝇 *S.*（*Robineauella*）*coei* 的系统发育位置。此外，最大简约分析和似然功能分析在 *scopariiformis-iwuensis* 进化枝和 *polystylata-hui* 进化枝的关系上产生了不一致的系统发育推断。因此，后续研究不仅需要其他的分子标记，也需要更多的分类取样。

关键词：贝叶斯分析；系统发育；Cytb 基因；COⅠ基因

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